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Decreased insect visitation to a native species caused by an invasive tree in the Cape Floristic Region

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ABSTRACT

Flowering invasive plants can potentially reduce pollination rates in co-flowering native plant species by attracting shared flower visitors. We investigate the effect of a prolifically flowering invasive species, *Acacia saligna* (Fabaceae), on native insect–flower interactions in surrounding communities. We surveyed flower visitation to *A. saligna* and selected native species at invaded and uninvaded areas and assessed the extent of flower visitor overlap of *A. saligna* and native species across four sites in South Africa's Cape Floristic Region. Median visitation rates of bees and all insects were significantly lower to one native species (*Roepera fulva*) in both field seasons at the same site when *A. saligna* was present. This native species also had the highest flower visitor overlap with *A. saligna* which was driven primarily by the native honeybee, *Apis mellifera* subsp. *capensis*. Observational data showed that *A. saligna* inflorescences were visited most frequently by minute beetles and the native honeybee. Our findings indicate that native honeybees are important visitors to *A. saligna*, and that at least one native plant species experiences reduced flower visitation due to competition with *A. saligna* for honeybee visits. Flowering *A. saligna* could have wide-reaching effects on native plants by competing for visits from a super generalist flower visitor – the native honeybee – which may jeopardize the reproductive success of natives whose flowering time overlaps with that of *A. saligna*. Our study further highlights the importance of understanding the effect of a flowering invasive species on native species and the potentially important mutualism between *A. saligna* and honeybees.

1. Introduction

Alien plants with showy floral displays are attractive to native pollinators and interact with co-flowering native plants, thereby becoming integrated into invaded ecosystems (Bartomeus et al., 2008; Geerts and Pauw, 2009; Lopezaraiza-Mikel et al., 2007; Memmott and Waser, 2002). Potential consequences of such integration include changes in native plant seed set, pollen deposition (Larson et al., 2006), pollinator abundance and diversity (Moroń et al., 2009), visitation rate (Bartomeus et al., 2008), or composition of the pollinator fauna (Muñoz and Cavieres, 2008). Previous studies have found evidence for facilitation of visitation to native plants (Moragues and Traveset, 2005) and increased pollinator richness and abundance (Bartomeus et al., 2008; Lopezaraiza-Mikel et al., 2007). However, a recent meta-analysis showed overall negative effects of flowering aliens on native plant pollination and reproduction (Morales and Traveset, 2009), which can further negatively impact plant and pollinator diversity (e.g. Gaertner et al., 2009; Moroń et al., 2009; Traveset and Richardson, 2006). For this reason and many others, invasive species are considered a major threat to biodiversity worldwide (Pimm et al., 1995). Management efforts are underway in many parts of the world to mitigate the harmful effects of invasive species (Pyšek and Richardson, 2010). Removal of aliens often has beneficial effects on native elements of ecosystems, but unexpected and sometimes undesirable effects have also been reported where, for instance, alien plants have become important resources for native pollinators (Carvalheiro et al., 2008; Valdovinos et al., 2009). More information on such interactions is needed to improve our ability to plan and execute effective restoration operations. Long-term effects of widespread flowering alien plants are poorly understood, but both positive and negative effects could potentially alter the evolutionary trajectories of native species and communities through pollinator shifts (Johnson et al., 1998; Schlüter et al., 2009). Consequently, understanding how a flowering alien plant interacts with co-occurring native plants and pollinators is important for developing plans for effective management interventions.

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Though research on this subject has increased over the last decade (Traveset and Richardson, 2011), most work has focused on alien shrubs or herbaceous species (e.g. *Impatiens*, *Lonicera*, *Lythrum*, *Solidago*), whereas some of the most problematic invasive species in many parts of the world are trees (e.g. *Acacia*, *Pinus*) (Lamarque et al., 2011; Richardson and Rejmánek, 2011). Australian *Acacia* species are a globally important group of plants. Many species have been widely introduced for their practical use (e.g. timber, fodder, land restoration), and many of these species have become invasive (Richardson et al., 2011). Australian acacias were introduced to South Africa, starting in the mid nineteenth century, mainly for tannin production and dune stabilization (Poynton, 2009). Many invasive *Acacia* species are now classified as "transformers" (invaders that change the character, condition, form or nature of ecosystems over a substantial area relative to the extent of that ecosystem; Richardson et al., 2000b) in South Africa (Henderson, 2001). They can completely alter the composition and diversity of native plant assemblages (Gaertner et al., 2011), change nutrient cycles (Yelenik et al., 2004) and fire regimes (van Wilgen and Richardson, 1985), thus radically altering the structure and functioning of ecosystems where invasion levels are high.

Although most invasive *Acacia* species grow well in disturbed areas, some species (e.g. *A. cyclops*, *A. longifolia*, *A. saligna*) can grow interspersed with native species, for instance in the sandy soils of lowland fynbos vegetation (see Fig. 1) (Yelenik et al., 2004). Moreover, the flowering time of some invasive species overlaps with that of many natives (Godoy et al., 2009). In many cases, the flower heads are long-lived with some able to last up to 2 weeks (George et al., 2009; Stone et al., 2003). *Acacia* species have a generalist floral morphology and form dense, bright floral displays during their flowering peak. In their native range, Australian acacias are visited most frequently by bees, wasps, flies and beetles (Bernhardt, 1989; Stone et al., 2003). Thus, there is a high potential for flowering acacias to interact with native communities via shared pollinators. Surprisingly, no studies have investigated the effect these species have on plant–pollinator relations in the communities they invade. Knowledge of such impacts can aid in the conservation of native plants and pollinators (Levy, 2011; Williams et al., 2010).

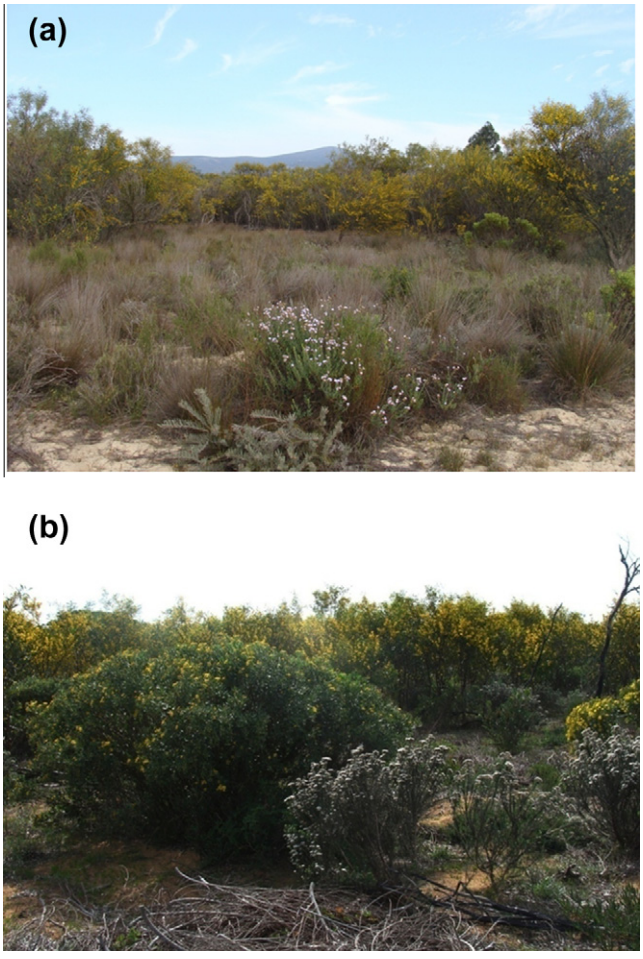

Fig. 1. (a) Floral display of *Acacia saligna* invading native fynbos vegetation in the Western Cape, South Africa (photo: A.M. Rogers). (b) Intermediate *Acacia saligna* invasion level in the background at the Koude Vlakte study site (photo: M.R. Gibson).

The aim of this study was to make a first assessment of the effect of a flowering invasive *Acacia* species on native plant–pollinator communities in South Africa. Specifically, we compare flower visitation and functional group composition of flower visitors to native species at sites where *Acacia saligna* is present and where it is absent. Visitation frequency has been shown to be an appropriate surrogate for both pollen transport (Alarcón, 2009) and the overall effect of animal mutualists on plant reproduction (Vázquez et al., 2005), and so may serve as a suitable first approximation of the overall effect of an invasive plant on native plant–pollinator communities. We also make the first assessment of visitors and visitation frequency to flowers of *A. saligna* in its introduced range, and calculate flower visitor overlap with native species. Due to its high abundance in many areas, its extensive, showy floral displays and easily accessible floral rewards (Gibson et al., 2011), we expected that *A. saligna* would likely compete with native species for flower visits on a community level as has been shown previously for other species (*Taraxacum officinale*–Muñoz and Cavieres, 2008; Real, 1983). Assuming that generalist insect foragers comprise a substantial portion of flower visitors to the invader (Memmott and Waser, 2002), we also expected that *A. saligna* would show at least moderate flower visitor overlap with native species.

2. Material and methods

2.1. Study area

The study took place in the south-western region of the Western Cape Province in South Africa's Cape Floristic Region (CFR). The CFR has one of the world's most diverse floras per unit area. The vegetation at our study sites is known as fynbos, and is dominated by species of Ericaceae, Proteaceae, and Restionaceae. The area receives about 500 mm of annual precipitation peaking in June through August, followed by the peak flowering season in spring (September–October) (Mucina and Rutherford, 2006). Mean summer and winter temperature extremes at our sites range from 27.9° C to 7.0° C, respectively. Important pollinators of native plants include mainly native bees (e.g. the Cape honeybee, *Apis mellifera* subsp. *capensis*), flies, and beetles (e.g. monkey beetles – Scarabaeidae: Rutelinae: Hopliini; Johnson, 2004).

The CFR also supports a high human density and so anthropogenic activities threaten much of its diversity, among which alien plant invasions are identified as the biggest threat (Rebelo, 2001; Rouget et al., 2003). Today invasive Australian acacias account for 36% cover of the lowlands in the Fynbos Biome (Rebelo et al., 2006). Our main study species is *A. saligna* (Labill.) H.L., an evergreen shrub or tree able to grow in sandy soils. Its bright yellow, globular inflorescences appear from August to November (Austral spring), and last up to 2 weeks (Stone et al., 2003). Despite major efforts to reduce the extent of invasive stands, especially over the past two decades (van Wilgen et al., 1994), *A. saligna* and several other Australian acacias still occur over tens of thousands of hectares (van Wilgen et al., 2011). Management of stands of invasive

woody plants is one of the biggest challenges facing conservation managers in the CFR (Roura-Pascual et al., 2009).

2.2. Sample design

We carried out flower visitor observations at four different sites over the spring months (August–September) of 2009 and 2010 (Table 1), with one site (Koude Vlakte) surveyed in both years. We surveyed an additional site for *A. saligna* flower visitors where the dominant plant species were grasses and *A. saligna* thicket. At each site, we located an area of native vegetation invaded by *A. saligna* ('invaded') and an adjacent, non-invaded area of native vegetation to serve as the control plot ('uninvaded'). In the invaded plots *A. saligna* coexisted with native species and formed noticeable and widespread floral displays (Fig. 1b). Sites ranged in size from approximately 25–130 ha in area. Invaded and uninvaded plots were more or less adjacent to one another with distances ranging from zero to 700 m, and sites were located at least 5 km apart. We surveyed both plot types to determine which flowering native species were relatively the most common and/or widespread (hereafter referred as 'focal species'). At each site three focal species were identified. Due to high levels of beta diversity in fynbos there was no overlap among sites in focal species. Ideally the same focal species should be present at different sites to account for site-specific differences that may influence insect visitation. Because focal native species are not replicated across study sites, results should be interpreted with caution.

2.3. Flower visitor observations

Visitor observations for each of the focal plant species were 'paired', and carried out simultaneously (within 30 min of one another) by two observers at invaded and uninvaded plots, to ensure constant climatic conditions. We conducted observations from roughly 08:00 until 17:00. Each focal species was observed at three different locations within a plot, located at least 60 m away from one another to reduce the influence of local effects. Observation times were rotated so that all three focal species were observed once per day during a different time period (08:00–11:00 = 'AM', 11:00–14:00 = 'MD', 14:00–17:00 = 'PM') to account for temporal variation of flower visitation. Each observation lasted 15–30 min so that each focal species was observed for a total of 90 min at each site. Large patches of each focal species were selected for observation. Within this larger patch, an area with 1-m radius (3.14 m^2) was selected where flower visitor identity and frequency were recorded and the number of focal flowers counted. Visitation was expressed as visits flower^{-1} h^{-1}. Observations of native species in the invaded plot took place <30 m from the nearest patch of *A. saligna*. Flower visitors not identifiable to species by eye in the field were collected for later identification. Time spent collecting flower visitors was not included in overall observation time, and visitors were collected using 'fynbos forceps' – consisting of two tea strainers tied to the end of a large pair of tongs – rather than sweep netting as the former causes less disruption. Floral visits were counted only if visitors made contact with the flower's reproductive parts, potentially transferring pollen.

2.4. Data analyses

To test whether unequal floral densities of focal species influenced flower visitation patterns between invaded and uninvaded plots, we quantified floral display size in invaded and uninvaded areas. We recorded number of floral displays, area of floral displays, number of floral 'units' per floral display and number of floral units per observation area within 30–50 m radius of each observation area (Appendix A). A floral display comprised a recognizable visual unit of conspecific flowers and referred to a single flower or group of flowers depending on the species (sensu Hegland and Totland, 2005). Floral display area was measured as the size of the flowering plant patch using one of three formulae: πr^2 if circular and vertically flat; length x width if rectangular; or $\pi r^2 + 2\pi r^2$ if circular with a depth dimension. A floral unit is a single flower head, or part of a multiple head, from which a medium size bee has to fly rather than walk to reach another floral unit of the same species (Dicks et al., 2002). We statistically compared floral parameters between all invaded and all uninvaded plots using the paired Wilcoxon signed rank test. We used R for all statistical analyses (R Development Core Team, 2011).

We compared insect visitation rate to focal species at invaded and uninvaded sites, where visitation rate is the number of visits flower^{-1} h^{-1}. We use visitation rate to account for the effect of floral density on visitation frequency. Because our data were non-parametric and contain many zeroes, we compared visitation rates of all flower visitors to all focal species across sites, each major flower visitor group to all focal species across all sites, and all flower visitors to individual focal species at each site, using a paired Wilcoxon signed rank test. Because sample sizes differed for focal species between field seasons (see Appendix B), we calculated one median visitation rate for each focal species ($N = 12$) when testing visitation differences of all focal species between invaded and uninvaded sites (Appendix C). We used individual focal species observations to calculate differences in visitation to individual focal species between invaded and uninvaded plots (Appendix B). We calculated functional group composition as the proportion of the total visitation rate comprised by each visitor group.

To test if field site was independent from difference in visitation rate to focal species between invaded and uninvaded plots, we used a generalized linear model with a Gaussian distribution and identity link because difference in visitation rate was normally distributed (Shapiro Wilk $W = 0.964$, $P = 0.762$). We divided flower visitors into groups based on their general functional differences, which, based on the subset of species we observed, refers to: beetles, flies, bees (small bees and native honeybees), other hymenoptera (wasps and ants), and other (all other insects). We did not group below family level for analyses involving visitation rate, as there were not enough representative individuals from each subgroup.

To find the flower visitor overlap of each focal species and *A. saligna*, we calculated the proportion of total visitation rate to a focal species that was comprised of visitor groups that also visited *A. saligna*. Flower visitor overlap was calculated on both a family- and morphospecies-level. Our sampling periods at each site resulted in unsaturated species-accumulation curves (not shown), thus we do not compare species richness or diversity between invaded and uninvaded sites. Because consecutive visits of most (non-bee) flower visitors were either non-existent or difficult to count, visitor abundance closely mirrored visitation frequency so visitor abundance is not reported here.

3. Results

Overall flower density parameters were not significantly different between invaded and uninvaded plots across all sites (Appendix D). However, at Mamre, there were significantly more floral displays ($N = 9$; $V = 33$; $P = 0.042$) and lower floral unit density ($N = 9$; $V = 1$; $P = 0.008$) for all focal species pooled at invaded plots than at uninvaded plots. Floral unit density of *Muraltia satureioides* was significantly higher ($N = 3$; $V = 21$; $P = 0.031$) and number of floral displays was nearly significantly lower ($N = 3$; $V = 0$; $P = 0.057$) at invaded plots.

Table 1
Study site locations, focal species, and floral display metrics used in this study. Statistic and p values for comparing vegetation parameters between invaded and uninvaded plots can be found in Appendix D.

Study site	GPS location	Focal species	Family	Median # floral displays/plot		Median area/floral display (m^2)		Median floral unit density/m^2	
				Invaded	Uninvaded	Invaded	Uninvaded	Invaded	Uninvaded
Mamre	33°31.3S	*Dimorphotheca pluvialis* (L.) Moench	Asteraceae	38	17	14.2	12.8	6.37	22.8
	18°29.2E	*Polycarena lilacina* Hilliard	Scrophulariaceae	36	1	2.47	7610	17.2	134
		Ursinia anthemoides (L.) Poir.	Asteraceae	1	10	4900	2480	13.1	48.6
Koude Vlakte	34°28.5S	*Chrysanthemoides monilifera*	Asteraceae	19.5	14.5	15.2	15.4	44.9	104
	19°26.7E	*Muraltia satureioides* DC.	Polygalaceae	8.5	14	60.5	18.9	94.4	46.2
		Roepera fulva (L.) Beier and Thulin	Zygophyllaceae	8.5	9	2.15	1.71	206	185
Witkrans	34°33.2S	*Erica parviflora* L. complex	Ericaceae	6	22	64.9	56.3	107	458
	19°27.5E	*Leucospermum patersonii* (L.) E.Phillips	Proteaceae	13	17	5.69	20.5	7.96	16.4
		Pelargonium betulinum (L.) L'Hér.	Geraniaceae	14	16	1.7	2.51	9.9	13
Walshacres	34°25.0S	*Erica imbricata* L. complex	Ericaceae	65	25	11.2	75.8	93.9	80.6
	19°25.9E	*Cyphia volubilis* (Burm.f.) Willd.	Campanuleaceae	28	46	0.031	0.083	191	103
		Mimetes cucullatus (L.) R.Br.	Proteaceae	38	8	4.69	6.61	2.86	5.09
Penhill	33°59.4S	*Acacia saligna* (Labill.) H.L. Wendl.	Fabaceae	n/a	n/a	n/a	n/a	n/a	n/a
	18°44.6E								

3.1. Paired tests

We found no significant difference in visitation rate of all insects or of individual visitor groups to focal species across all sites (Table 2). When testing for differences of flower visitors to individual focal species at each site, we found that visitation rates of all insects and bees were significantly higher to *Roepera fulva* at uninvaded sites (Table 2). Beetle visitation to *Leucospermum patersonii* was marginally higher at invaded versus uninvaded plots. The proportion of overall visitation rate comprised by each visitor group at all invaded and uninvaded sites is presented in Fig. 2. No significant differences were found between invaded and uninvaded sites for any group (chi-squared = 0.396, $df = 5$, $P = 0.995$).

Results of the generalized linear model indicated that site had no effect on change in visitation rate of all visitor groups between invaded and uninvaded plots.

3.2. Acacia flower visitors

A. saligna was visited most frequently by beetles (60% of total visitation rate; avg = 0.145 ± 0.021 visits flower^{-1} h^{-1}), followed by native honeybees (*A. mellifera* subsp. *capensis*; 26% of total visitation rate; avg = 0.061 ± 0.023 visits flower^{-1} h^{-1}) and flies (9% of total visitation rate; avg = 0.023 ± 0.006 visits flower^{-1} h^{-1}) across all sites (including the *Acacia*-only site, Penhill; Fig. 3). The families Nitidulidae, Mordellidae, Melyridae, and Scarabaeidae comprised 61% of all beetle visits, and calyptrate flies (mostly from family Rhiniidae) comprised approximately 63% of all fly visits (Table 3). When comparing flower visitor composition on *A. saligna* inflorescences between sites, proportion of visits made by major visitor groups (beetles, flies, and honeybees) differed markedly (chi-squared = 233, $df = 10$, $P < 2.2e{-}16$; Fig. 4). At Mamre, where honeybees were absent during our survey, about 40% of the total visitation rate to *A. saligna* was made by Diptera, mainly of family Rhiniidae, and about 60% by small beetles of five main families (Melandryidae, Anthicidae, Mordellidae, Nitidulidae, and Melyridae). Visitor group proportions were roughly similar at Koude Vlakte (both years) and Witkrans, but were dominated at Walschacres by beetles from families Nitidulidae and Tenebrionidae and at Penhill by beetles in the families Scarabaeidae, Mordellidae, and Melyridae. A list of all visitors to *A. saligna* can be found in Table 3. Additionally, 26% of the total visitation rate to *A. saligna* inflorescences was made by flower visitors (39/56 morphospecies) not found on any of the focal species across all sites (see Appendix E).

3.3. Flower visitor overlap with A. saligna

Flower visitor overlap with *A. saligna* was highest in the native plant species *R. fulva* (88% of total visitation rate, 2009 field season), and *Pelargonium betulinum* (61%), mainly due to the shared flower visitor *A. mellifera* subsp. *capensis* (Appendix E). Overlap at the family level was highest with *R. fulva* (95%, 2009 field season), *Dimorphotheca pluvialis* (91%), *L. patersonii* (87%), and *R. fulva* (83%, 2010 field season) due to sharing of the families Apidae, Bombyliidae and Scraptiidae, Formicidae and Apidae, and Apidae, respectively.

4. Discussion

Visitation rates of all insects and bees to the focal species *R. fulva* (Fig. 5) were significantly lower in invaded plots than in uninvaded plots in both years of our study, removing the possibility that *A. saligna* invasion acts to increase overall resource availability and faciliate visitation to native species. Results also suggest that *R. fulva* may suffer from floral competition with *A. saligna*. The fact that honeybees were found to visit *A. saligna* inflorescences frequently further supports the idea that the alien's overwhelming floral display at invaded sites could be attracting bee visits away from *R. fulva*. In contrast, a higher beetle visitation rate to *Leucospermum patersonii* at invaded plots could indicate a facilitative interaction with *A. saligna*. However, this is less likely as beetles are not suggested to be an important visitor group in terms of proportion of total visitation rate to *L. patersonii* (Appendix E) and were largely sedentary, moving little between flowers (excluding Scarabaeidae: Hopliini beetles).

The high number of beetles found visiting *A. saligna* inflorescences is likely inflated because this number included small beetles that were present on the flowers before the observation began and remained on or in the inflorescences during the observation. Thus, most of the beetle individuals counted were sedentary or moved within the same inflorescence during the course of our observation. This does not discount their importance as potential pollinators. The most important visitors to *A. saligna* inflorescences are probably native honeybees, as they are the most frequent and mobile flower visitors. This is in line with other studies of Australian *Acacia* flower visitors in the plants' introduced ranges (Alves and Marins-Corder, 2009; Sornsathapornkul and Owens, 1998; J.G. Rodger, unpubl. data) and suggests that honeybees may be important in cross-pollination (Stone et al., 2003), though this remains to be formally tested. Our results also concur with a growing body of

literature reporting the importance of honeybees in the pollination and spread of invasive flowering plants (Barthell et al., 2001; Gross et al., 2010; Richardson et al., 2000a; Stout et al., 2002). Our observations of the broad spectrum of visitors to *A. saligna* adds support for the idea that the spread of invasive plant species is often not limited by a lack of suitable pollinators (Richardson et al., 2000a). Strong interactions between the native honeybee, *A. mellifera* subsp. *capensis*, and *A. saligna* are of concern because the honeybee is a generalist and visits many flowering fynbos species. Thus, usurpation of this pollinator by *A. saligna* could have far-reaching effects in the native plant community and significantly alter pollination network structure (Aizen et al., 2008). Interactions between farmed honeybees and flowering *A. saligna* are important to consider as they contribute to total *Acacia* visitation and could contribute toward *Acacia* pollination and reproduction success. Similarly, *A. saligna* could be providing farmed honeybee populations with an important forage resource.

The finding of different *Acacia* flower visitor assemblages between sites may reflect site differences in vegetation type, structure, and native species richness. Variation in visitor assemblage further highlights the lack of specificity in *A. saligna*'s relations with flower visitors. We recommend that future studies investigate the consequences of such variation for *Acacia* seed set. The fact that the majority of morphospecies found on *A. saligna* inflorescences were not found on any of the focal species would suggest low potential flower visitor overlap; however, 30% of the total visitation rate to *A. saligna* was comprised by native honeybees, which also visited many of the focal species. Therefore, flower visitor overlap was still relatively high based on a shared generalist flower visitor.*R. fulva* had by far the highest morphospecies overlap with *A. saligna* compared to other focal species, indicating that this species may be vulnerable to changes in flower visitation when *A. saligna* is present. This prediction is supported by our results from the Wilcoxon's paired test that showed a significantly lower visitation rate of insects to this focal species when *A. saligna* was present across both years. The fact that flower visitor overlap between *R. fulva* and *A. saligna* is driven primarily by the native honeybee has important implications for other native species that are frequently visited by honeybees. In addition to reduced visitation rates, species that share honeybees with *A. saligna* may suffer from improper

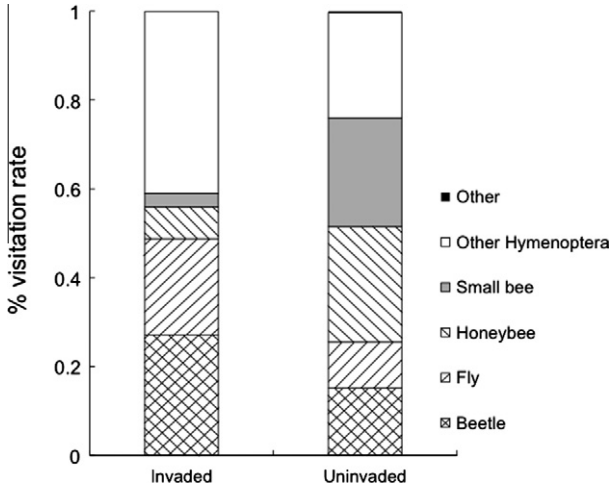

Fig. 2. Composition of flower visitor groups observed on focal native species in invaded and uninvaded plots showing the proportion of total visitation rate (visits flower^{-1} h^{-1}) comprised by each group.

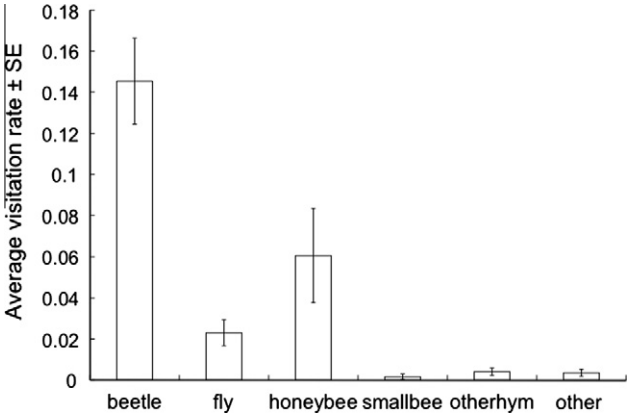

Fig. 3. Average visitation rates (visits flower^{-1} h^{-1}) of flower visitor groups to *Acacia saligna*. otherhym = other hymenoptera.

Table 2
Wilcoxon ranked sum test results comparing visitation rate between invaded (I) and uninvaded (U) plots. Only significant results are presented.

Variables tested between invaded and uninvaded plots			Median visitation rate (visits flower^{-1} h^{-1})		
Focal species	Visitor group	*N*	I	U	Result
All	All	12	0.31	0.23	$V = 46$ $P = 0.622$
	Beetles	12	0.079	0.009	$V = 53$ $P = 0.301$
	Flies	12	0.047	0.034	$V = 51$ $P = 0.380$
	Honeybees	12	0.089	0.179	$V = 8$ $P = 0.375$
	Small bees	12	0.027	0.063	$V = 11.5$ $P = 0.400$
	Other hymenoptera	12	0.019	0.018	$V = 33$ $P = 0.25$
Roepera fulva (2009 and 2010)	All	9	0.476	0.879	$V = 3$ $P = 0.020$
Roepera fulva (2009 and 2010)	Honeybees	9	0.011	0.86	$V = 7$ $P = 0.074$
Roepera fulva (2009 and 2010)	All bees	9	0.234	0.875	$V = 5$ $P = 0.039$
Erica parviflora	Honeybees	6	0.089	0	$V = 20$ $P = 0.063$
Leucospermum patersonii	Beetles	5	0.235	0	$V = 15$ $P = 0.059$

Table 3
List of flower visitors to *Acacia saligna* at five study sites in the Western Cape, South Africa.% columns refer to (left to right): the proportion of all visits made by the given visitor order; the proportion of all order visits made by the given visitor family.

Order	% of total visits	Family	% of order visits	Morphospecies
Coleoptera	61.6	Anthicidae	5.68	*Anthicus* sp.
				Formicomus sp.
				Notoxus sp.
		Bruchidae	0.20	Bruchidae sp.
		Chrysomelidae	1.76	Cryptocephalinae sp.
				Eumolpinae sp.
				Galerucinae sp.1
				Galerucinae sp.2
				Galerucinae sp.3
		Cryptophagidae	0.39	Cryptophagidae sp. '18'
				Cryptophagidae sp. 'cry'
		Curculionidae	4.31	Unidentified
				Melanterius sp. (control agent)
				Ceutorhynchini sp.
				Ceutorhynchus sp.1
				Ceutorhynchus sp.2
				Derolomus sp.
				Tychius sp.
		Dermestidae	2.94	Dermestidae sp. '7'
				Dermestidae sp. '7A'
				Dermestidae sp. '7C'
				Anthrenus sp.
		Elateridae	0.98	*Calais* sp.
		Melandryidae	7.63	Melandryidae sp.
		Melyridae	13.5	Melyridae sp. '8'
				Melyridae sp. '8-1'
				Melyridae sp. '9'
				Melyridae sp. 'M
		Mordellidae	16.4	Unidentified
				Anaspis sp.1
				Anaspis sp.2
				Anaspis sp.3
				Anaspis sp.4
		Nitidulidae	21.1	Unidentified
				Aethina sp.
				Carpophilus sp.
				Meligethes sp.
				Pria sp.
		Scarabaeidae	10.0	Unidentified
Coleoptera		Scarabaeidae		Rutelinae: Hopliini misc
				Rutelinae: Hopliini sp. '10C'
				Rutelinae: Hopliini sp. '10S2'
				Rutelinae: Hopliini sp. 'black and white'
				Rutelinae: Hopliini sp. 'orange'
		Scraptiidae	1.17	Scraptiidae sp. '1'
				Scraptiidae sp. '1A'
		Tenebrionidae	7.44	*Statira* sp.
		Unidentified	6.46	
Diptera	8.09	Bibionidae	1.49	Bibionidae sp. 'Bib4'
		Bombyliidae	5.97	Unidentified
				Bombyliidae sp.4
				Bombyliidae sp.6
		Calliphoridae	2.99	Unidentified
				Calliphoridae sp. '4B'
		Cecidomyiidae	5.97	Cecidomyiidae sp. '6'
		Empididae	2.99	Unidentified
				Empididae sp. 'E'
		Muscidae	1.49	Muscidae sp. '4C'
		Phoridae	1.49	Phoridae sp. 'P'
		Rhiniidae	56.7	Rhiniidae sp. 1
				Rhiniidae sp. 2
				Cosmina sp.
		Scathophagidae	1.49	Scathophadidae sp.
		Sciaridae	5.97	Sciaridae sp. '7'
		Unidentified	13.4	
Hemiptera	0.60	Anthocoridae	60.0	Anthocoridae sp. 'anth'
		Rhopalidae	20.0	Rhopalidae sp.1
		Unidentified	20.0	
Hymenoptera	28.5	Apidae	94.1	*Apis mellifera* subsp. *capensis*
				Braunsapis sp.
		Eulophidae	0.85	*Tetrastichus* sp.
		Formicidae	1.69	*Camponotus niveosetosus*
				Tetraponera sp.1

(*continued on next page*)

Table 3 (*continued*)

Order	% of total visits	Family	% of order visits	Morphospecies
		Halictidae	0.42	*Lasioglossum* sp.
		Platygastridae	0.42	Platygastridae sp.
		Unidentified	2.54	
Lepidoptera	0.36	Unidentified	100	
Thysanoptera	0.85	Unidentified	100	

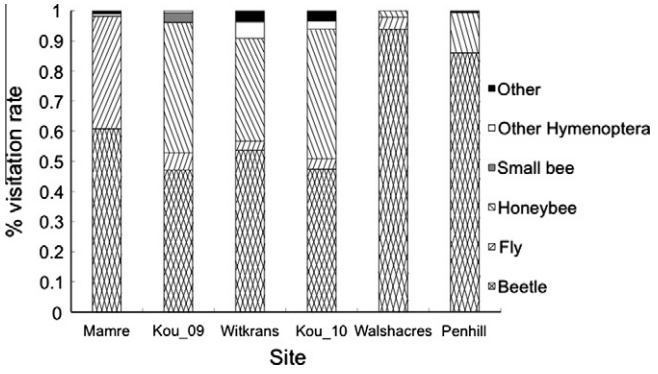

Fig. 4. Composition of flower visitor groups found on *Acacia saligna* at each study site showing the proportion of total visitation rate (visits flower^{-1} h^{-1}) comprised by each group.

Fig. 5. The focal native species, *Roepera fulva*, at the Koude Vlakte field site had the highest flower visitor overlap with *Acacia saligna* primarily due to the shared visitor *Apis mellifera* subsp. *capensis*, the native honeybee (photo: M.R. Gibson).

pollen transfer resulting in stigma clogging and pollen loss to heterospecific stigmas (Larson et al., 2006). These latter effects are an interesting avenue for future research on the effects of *A. saligna* on native flowering plants.

5. Conclusions

The effect of *A. saligna* on insect visitation to co-flowering taxa was both species- and site-specific in our study. Consequently, we suggest that drawing conclusions on *A. saligna*'s effect on natives at a community level requires further investigation. However, the strong effect of *A. saligna* on honeybee visitation rates at co-flowering natives suggests that *Acacia* invasion may have wide-reaching impacts on the pollination and reproductive success of many co-flowering native communities, especially since bees are the most important pollinators for many flowering species (Faegri and van der Pijl, 1979; Johnson, 2004). Additional measurements of the effect of *A. saligna* on interspecific pollen transfer within native communities, and its effect on seed set in native species, are needed. Furthermore, honeybees are generalist foragers that can facilitate the invasion of flowering alien plants (Gross et al., 2010), and more research is needed to determine their contribution to *A. saligna* pollination and reproductive success.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.07.011.

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